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Effects of temperature on flowering phenological traits of *Populus euphratica* Oliv. and *Populus pruinosa* Schrenk populations, Xinjiang, China

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Abstract: The aims of this study were to explore the interspecific differences of *Populus euphratica* Oliv. and *Populus pruinosa* Schrenk populations and the intraspecific differences of males and females within the same species in flowering phenological traits, and the effects of temperatures on flowering phenological traits in different growth years (2001–2003 and 2013–2015). The results showed that *P. euphratica* population flowered earlier than *P. pruinosa* population. Moreover, flowering phenological period of population, number of days of flowering phenological period per population, number of days of flowering phenological period per plant and average number of days of flowering period per plant of *P. euphratica* population were less than those of *P. pruinosa* population. The differences between male and female within the same species indicated that the flowering periods of males *P. euphratica* and *P. pruinosa* populations were earlier than those of female plants. For both species, flowering phenological traits were significantly and negatively correlated with the average temperatures in previous ten days, previous one month and previous three months of flowering. Both species are sensitive to temperature changes and adjust to the changes by advancing the start of flowering and prolonging the duration of flowering.

Keywords: *Populus euphratica* Oliv.; *Populus pruinosa* Schrenk; flowering phenology; temperature; flowering synchrony

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1 Introduction

Plant phenology refers to the growth and development that present seasonal changes in plants within a year. Phenology includes leaf sprouting, leaf expansion, flowering, leaf colour change and leaf fall (Lu et al., 2006). Ultimately, phenology reflects the growth and developmental rhythm that is gradually established during a plant's long-term adaptation to seasonal changes in its environment (Zhang et al., 2004). Plant flowering phenology is especially relevant to reproductive processes and includes various traits, such as flower bud formation and development, early flowering stage, full-bloom stage, and flowering duration (Whitehead, 1983). For example, the early flowering stage and flowering synchrony have been demonstrated to be very important to plant reproductive success (Rathcke and Lacey, 1985). In particular, flowering synchrony not only is a major factor that increases the probability of reproductive success (Waser, 1978; Thomson, 1980), but also contributes to a general tendency of plants to adopt earlier flowering as conditions permit (Campbell, 1989; Kelly, 1992). The first and last dates of flowering determine

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the duration of flowering, flowering intensity and flowering synchrony. Moreover, other flowering traits are closely related to seed yield and quality (Zhang and Chen, 2001; Xiao et al., 2004). Thus, flowering phenology plays an important role in the development of viable seeds and in achieving reproductive success for the successful survival of plant populations.

A number of studies have focused on phenologies in different regions and species (Primack, 1980; Marquis, 1988; Guitian and Sanchez, 1992; Tarasjev, 1997; Abe, 2001; Rosenzweig et al., 2007; Fan et al., 2016). Studies based on field phenological records in Europe (Menzel et al. 2006), Asia (Ho et al., 2006; Doi, 2012; Ge et al., 2015; Tao et al., 2017) and North America (Wolfe et al., 2005; Gonsamo et al., 2013) revealed a trend of earlier occurrence of the spring phenophase, including an early leaf expansion and early flowering for major woody plants. Meanwhile, other studies have reported that in temperate regions in China, the early occurrence of the spring phenophase has been mainly attributed to the observed increases in temperature (Rosenzweig et al., 2008; Polgar et al., 2011). Temperatures measured at 16 meteorological stations across eastern China over several months just prior to the spring phenophase were found to be correlated with phenological traits (Zheng et al., 2006). Moreover, results demonstrated that woody plant phenology was mainly influenced by temperature and not by precipitation or sunlight (Zhang, 1995). Other related studies have also underscored the importance of previous temperature in the initial flowering period (Bolmgren et al., 2013; Dai et al., 2013; Wang et al., 2015; Xu et al., 2017). For example, with increased mean temperature during the months just before flowering, the first flowering dates of 4 plant species in Hungary significantly advanced by average ranges of 1.9–4.4 d/10a (Szabó et al., 2016), the first flowering dates of 48 woody plants during 1963–2007 in Beijing advanced by 0.2–5.3 d/10a (Bai et al., 2011), and the first flowering dates of 19 plants during 2001–2012 in Canada advanced by 2.0–22.0 d/10a (Gonsamo et al., 2013). Under climate change, the main reason underlying differences in phenological changes among species can be attributed to differences in the sensitivity of plant responses to temperature changes (Rosenzweig et al., 2008; Polgar et al., 2011).

Populus euphratica Oliv. and *Populus pruinosa* Schrenk, which are members of the Salicaeae family, are woody plants that reproduce via wind-borne pollen. About 91.1% of *P. euphratica* and *P. pruinosa* grow along the Tarim River Basin, Xinjiang, China (Wang, 1995). Both species play important roles in maintaining regional ecosystem equilibrium. Amongst the phenophases of these species, flowering duration is the shortest, while fruit maturation period is the longest (Wang, 1995; Maryamgul et al., 2016). Zhou et al. (2005) investigated variations in flowering phenologies of *P. euphratica* and *P. pruinose* and found that male plants of both species exhibited earlier flowering phenology than female plants. Moreover, both male and female *P. euphratica* plants exhibited earlier flowering phenology than *P. pruinosa* plants. Notably, other studies suggest that the first flowering dates may be significantly correlated with temperatures (Bolmgren et al., 2013; Dai et al., 2013; Wang et al., 2015; Xu et al., 2017). However, these studies did not address whether these temporal changes were due to temperature changes in earlier periods. Therefore, the aims of this study were to determine how the flowering phenological traits of *P. euphratica* and *P. pruinosa* populations vary in different years, and to correlate phenology with temperature variations.

2 Materials and methods

2.1 Materials

The study area was in the mixed forest of *P. euphratica* and *P. pruinosa* populations in the Aral City, Xinjiang, China (40°29′N, 80°50′E; 1023 m a.s.l.), and the sample area was 100 m^2. We selected 3 representative plots in the mixed forest. Trees of different genders were counted and measured within the 3 sample plots to determine the average diameter at breast height and average height. Within each sample plot, trees presenting an average diameter at breast height, non-biased and well-balanced crowns were selected as the sample trees. To better reflect the differences in flowering phenophases between males and females as well as their overlap duration, we chose 30 male trees and 30 female trees of the same age for each species, and then we labelled them with scutcheon tags for phenological observations. Table 1 shows the characteristics of the

forest stand.

Table 1 Characteristics of the forest stand in sampling plots

Tree species and gender	Tree age (a)	Diameter at breast height (cm)	Tree height (m)	Clear bole height (m)	Canopy closure
P. euphratica♂	20	14.68	8.17	1.81	0.68
P. euphratica♀	20	12.11	8.17	2.09	0.72
P. pruinosa♂	20	14.88	7.73	1.76	0.65
P. pruinosa♀	20	13.67	7.62	1.70	0.75

2.2 Flowering phenology measurement

The flowering phenology of plants includes the flower bud sprouting period (from the flower bud expansion to bud scales cracking), flower bud debarking period (from the bud scales cracking to inflorescence elongation), flowering period (from inflorescence elongation to powder dropping), inflorescence drooping period and wilting period (Zhou et al., 2005).

The flowering phenological period per plant refers to the duration when flower buds begin to expand to the end of the male flower powder or female flower stigma wilting of each plant. The flowering phenological period per population refers to the duration from when the first flower bud sprouts to when the last plant finishes flowering of each population. Flowering phenological period of population refers to the period from when the first plant in the population begins flowering to when the last plant finishes flowering.

According to the definition of flowering phenology, we observed every plant on the flower bud sprouting period, flower bud disbarking period, and flowering period from March to April during 2001–2003 and 2013–2015.

2.3 Meteorological data

Meteorological data were obtained from the meteorological station in the Aral City, Xinjiang, China.

2.4 Statistical analysis

We used SPSS 13.0 (SPSS 13.0 J Base System, 2005, SPSS Japan Inc., Tokyo) to calculate the Pearson correlation coefficient and conduct correlation analyses.

3 Results

3.1 Flowering phenological traits of *P. euphratica* and *P. pruinosa* populations in different years

Tables 2 and 3 showed that the flowering phenological period of *P. euphratica* population was earlier than that of *P. pruinosa* population for all years. Compared with *P. euphratica* population, *P. pruinosa* population exhibited higher flowering phenological period of population, number of days of phenological flowering period per population, number of days of flowering phenological period per plant and average number of days of flowering period per plant. Moreover, the first flowering date and the last flowering date of male plants were both earlier than those of female plants for both *P. euphratica* and *P. pruinosa* populations.

The first flowering dates of *P. euphratica* and *P. pruinosa* populations started from 14 March to 22 March during 2001–2003 and from 12 March to 18 March during 2013–2015. This result suggests the first flowering dates of both species during 2013–2015 were earlier than those of during 2001–2003. The similar trend was observed for the last flowering dates for both species across the same time period.

3.2 Flowering phenological traits of male and female *P. euphratica* and *P. pruinosa* populations in different years

In each year, the first and last flowering dates of male plants for both species were earlier than

Table 2 Flowering phenological traits of *P. euphratica* and *P. pruinosa* populations during 2001–2003

Year	Species and gender	Flowering phenological period of population	Number of days of flowering phenological period per population (d)	Number of days of flowering phenological period per plant (d)	Average number of days of flowering period per plant (d)
2001	*P. euphratica*♂	15 Mar–12 Apr	29	19	8
	P. euphratica♀	17 Mar–16 Apr	31	21	10
	P. pruinosa♂	18 Mar–17 Apr	31	20	10
	P. pruinosa♀	20 Mar–20 Apr	32	22	13
2002	*P. euphratica*♂	17 Mar–16 Apr	30	19	9
	P. euphratica♀	19 Mar–18 Apr	31	20	11
	P. pruinosa♂	20 Mar–18 Apr	30	20	10
	P. pruinosa♀	22 Mar–22 Apr	32	23	13
2003	*P. euphratica*♂	14 Mar–10 Apr	29	19	8
	P. euphratica♀	17 Mar–11 Apr	31	20	10
	P. pruinosa♂	18 Mar–17 Apr	30	19	11
	P. pruinosa♀	20 Mar–21 Apr	31	21	11

Table 3 Flowering phenological traits of *P. euphratica* and *P. pruinosa* populations during 2013–2015

Year	Species and gender	Flowering phenological period of population	Number of days of flowering phenological period per population (d)	Number of days of flowering phenological period per plant (d)	Average number of days of flowering period per plant (d)
2013	*P. euphratica*♂	12 Mar–6 Apr	25	15	7
	P. euphratica♀	16 Mar–11 Apr	27	17	7
	P. pruinosa♂	14 Mar–8 Apr	26	16	9
	P. pruinosa♀	16 Mar–12 Apr	28	20	10
2014	*P. euphratica*♂	13 Mar–7 Apr	26	16	6
	P. euphratica♀	16 Mar–11 Apr	27	18	8
	P. pruinosa♂	15 Mar–11 Apr	28	16	8
	P. pruinosa♀	18 Mar–15 Apr	29	19	9
2015	*P. euphratica*♂	12 Mar–7 Apr	27	19	7
	P. euphratica♀	15 Mar–11 Apr	28	20	8
	P. pruinosa♂	14 Mar–10 Apr	28	18	8
	P. pruinosa♀	16 Mar–14 Apr	30	19	10

those of female plants (Tables 4 and 5). For *P. euphratica* populations, the average first flowering date of female plants was 2 d later than that of male plants, while the average last flowering date of the female plants was 4 d later than that of male plants. For *P. pruinosa* population, the first flowering date of female plants was 1 d later than that of male plants, while the last flowering date of female plants was 3 d later than that of male plants. These results suggest that male plants exhibit longer flowering periods than female plants, thus being significant for the successful completion of pollination and fertilisation. Tables 4 and 5 showed different trends in both flowering overlapping periods and number of days of male and female plants flowering overlap of two species during 2001–2003 and 2013–2015.

In this study, the number of flowering plants reflected changes in the quantity of flowering plants during flowering phenophase, as shown in Figures 1 and 2. Differences were observed in the number of flowering plants over time and the peak number of flowering plants of each species in different years. For example, the numbers of female and male flowering plants in different

years displayed two-peak and one-peak profiles for *P. euphratica* and *P. pruinosa* populations, respectively, over time. Similar features included the duration of the peak flowering period of the *P. euphratica* population, which was longer than that of the *P. pruinosa* population. From the changes in the numbers of male and female flowering plants, the flowering periods of male and female *P. euphratica* and *P. pruinosa* populations had a longer time overlap.

Table 4 Overlap in flowering periods of male and female *P. euphratica* and *P. pruinosa* populations during 2001–2003

Year	Species and gender	Flowering period of population	Number of days of flowering period per Population (d)	Male and female flowering overlapping period	Number of days of male and female flowering overlap (d)
2001	*P. euphratica*♂	23 Mar–6 Apr	15	25 Mar–6 Apr	13
	P. euphratica♀	25 Mar–10 Apr	17		
	P. pruinosa♂	26 Mar–12 Apr	18	28 Mar–12 Apr	16
	P. pruinosa♀	28 Mar–15 Apr	19		
2002	*P. euphratica*♂	24 Mar–7 Apr	15	26 Mar–7 Apr	13
	P. euphratica♀	26 Mar–11 Apr	17		
	P. pruinosa♂	27 Mar–11 Apr	16	29 Mar–11 Apr	14
	P. pruinosa♀	29 Mar–16 Apr	19		
2003	*P. euphratica*♂	22 Mar–4 Apr	14	25 Mar–4 Apr	11
	P. euphratica♀	25 Mar–9 Apr	16		
	P. pruinosa♂	26 Mar–10 Apr	16	29 Mar–10 Apr	13
	P. pruinosa♀	29 Mar–14 Apr	18		

Table 5 Overlap in flowering periods of male and female *P. euphratica* and *P. pruinosa* populations during 2013–2015

Year	Species and gender	Flowering period of population	Number of days of flowering period per Population (d)	Male and female flowering overlapping period	Number of days of male and female flowering overlap (d)
2013	*P. euphratica*♂	20 Mar–31 Mar	12	23 Mar–31 Mar	9
	P. euphratica♀	23 Mar–4 Apr	13		
	P. pruinosa♂	22 Mar–4 Apr	14	24 Mar–4 Apr	12
	P. pruinosa♀	24 Mar–8 Apr	16		
2014	*P. euphratica*♂	21 Mar–31 Mar	11	24 Mar–31 Mar	8
	P. euphratica♀	24 Mar–5 Apr	13		
	P. pruinosa♂	23 Mar–4 Apr	12	25 Mar–4 Apr	11
	P. pruinosa♀	25 Mar–8 Apr	15		
2015	*P. euphratica*♂	20 Mar–29 Mar	11	23 Mar–29 Mar	7
	P. euphratica♀	23 Mar–4 Apr	13		
	P. pruinosa♂	23 Mar–4 Apr	13	25 Mar–4 Apr	11
	P. pruinosa♀	25 Mar–8 Apr	15		

3.3 Effects of temperature on flowering phenological periods of *P. euphratica* and *P. pruinosa* populations

Table 6 revealed significant or extremely significant negative correlations between flowering phenological traits and temperature. The number of days of flowering phenological period per population was significantly influenced by the average temperatures in previous ten days and previous one month of flowering. The number of days of flowering phenological period per plant was significantly influenced by the average temperature in previous one month of flowering. The average number of days of flowering period per plant was significantly influenced by the average

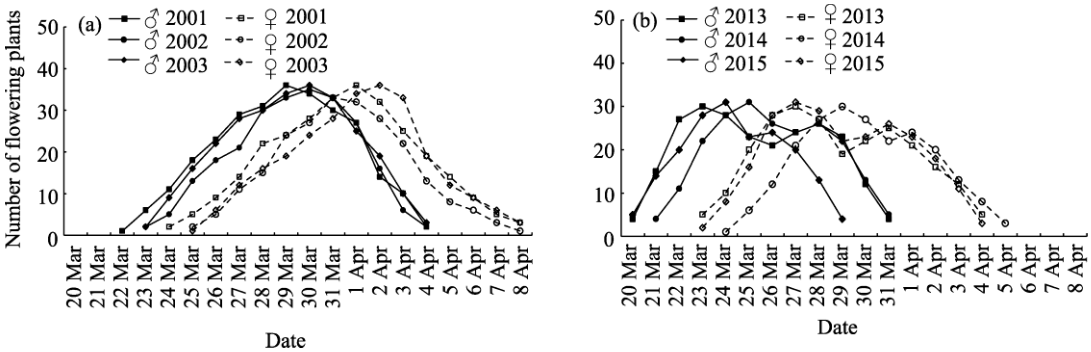

Fig. 1 Changes in the numbers of flowering plants of male and female *P. euphratica* population

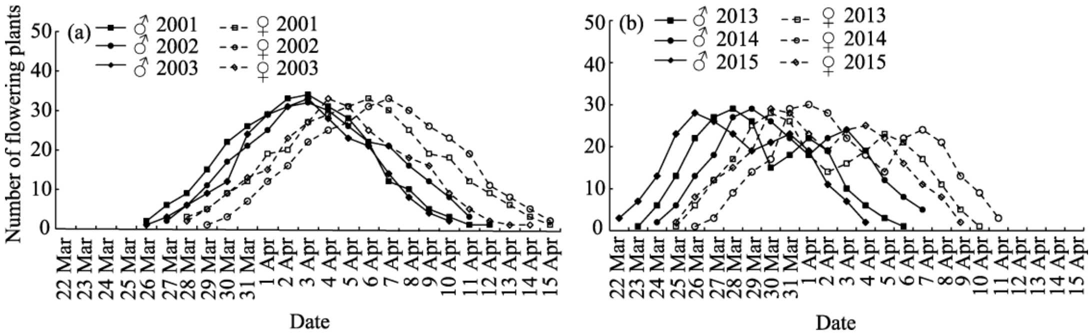

Fig. 2 Changes in the numbers of flowering plants of male and female *P. pruinosa* population

Table 6 Relationships between flowering phenological traits of *P. euphratica* and *P. pruinosa* populations and temperatures

Species and gender	Flowering phenological trait	Average temperature in previous ten days	Average temperature in previous one month	Average temperature in previous three months	Average temperature in whole flowering period
P. euphratica♂	Number of days of flowering phenological period per population	–0.96**	–0.90**	–0.72	–0.89**
	Number of days of flowering phenological period per plant	–0.83*	–0.77*	–0.79*	–0.74
	Average number of days of flowering period per plant	–0.84*	–0.92**	–0.71	–0.98**
P. euphratica♀	Number of days of flowering phenological period per population	–0.95**	–0.76*	–0.77*	–0.94**
	Number of days of flowering phenological period per plant	–0.88**	–0.90**	–0.82*	–0.92**
	Average number of days of flowering period per plant	–0.97**	–0.78*	–0.70	–0.97**
P. pruinosa♂	Number of days of flowering phenological period per population	–0.97**	–0.84*	–0.84*	–0.88**
	Number of days of flowering phenological period per plant	–0.79*	–0.90**	–0.74	–0.77*
	Average number of days of flowering period per plant	–0.85*	–0.83*	–0.85*	–0.94**
P. pruinosa♀	Number of days of flowering phenological period per population	–0.90**	–0.71	–0.82*	–0.90**
	Number of days of flowering phenological period per plant	–0.84*	–0.96**	–0.77*	–0.85*
	Average number of days of flowering period per plant	–0.81*	–0.74	–0.79*	–0.85*

Note: * and ** indicate significances at $P<0.05$ and $P<0.01$ levels, respectively.

temperature in whole flowering period (Table 6). For both species, a higher temperature was associated with lower number of days of flowering phenological period per population, number of days of flowering phenological period per plant, and average number of days of flowering period per plant. These results suggest that changes in temperature in the early stage can influence the first flowering date and the duration of flowering period.

By comparing the average temperatures for a given period (Figs. 3 and 4), we found no significant temperature difference within the corresponding periods of 2001–2003 and 2013–2015. However, the temperatures in previous ten days and previous one month of flowering during 2001–2003 were lower than those of during 2013–2015. These results can explain why the first flowering date during 2013–2015 was earlier than that of during 2001–2003, suggesting that the differences in flowering phenological period were caused by the differences in average temperatures at the same period.

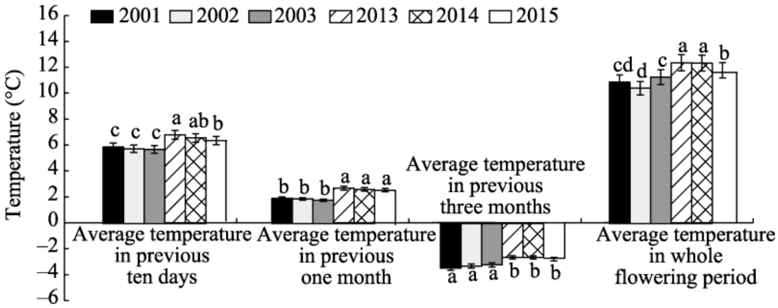

Fig. 3 Differences in average temperatures in previous ten days, previous one month, previous three months, and whole flowering period of *P. euphratica* population in different years. Different lowercase letters indicate significance at different years in the same period at $P<0.05$ level. Bars mean standard errors.

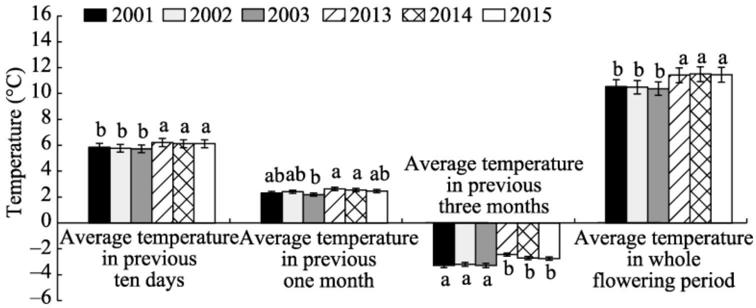

Fig. 4 Differences in average temperatures in previous ten days, previous one month, previous three months and whole flowering period of *P. pruinosa* population in different years. Different lowercase letters indicate significance at different years in the same period at $P<0.05$ level. Bars mean standard errors.

4 Discussion

4.1 Flowering phenological traits of *P. euphratica* and *P. pruinosa* populations under the same environmental condition

Previous studies have reported that six different populations of *P. euphratica* plants exhibited lower differences in the flowering phenological period, with an earlier flowering dates of male plants than that of female plants, a longer duration of flowering of female plants than that of male plants, and a longer flowering period overlap of male and female plants (Zhang et al., 2004; Zhou et al., 2005; Maieryanguli et al., 2016). In this study, we found that the first flowering date of *P. euphratica* population was earlier than that of *P. pruinosa* population in all years, thus further emphasizing the differences in flowering phenology between the two species under the same environmental condition.

For both *P. euphratica* and *P. pruinosa* populations, the first flowering date of male plants was earlier than that of female plants in all years. However, results revealed that female plants

exhibited higher flowering phenological period of population, number of days of flowering period per population, number of days of flowering phenological period per plant, and average number of days of flowering period per plant compared with male plants. These results suggest that for both species, female plants have a longer flowering period than male plants, which could help reduce the risk of pollination failure due to a short time of pollination caused by rapid climate change and a lack of wind.

Within a population, the length of the overlap period, in which the pollen dispersal period of male plant overlaps with the reproductive period of female plant, is of great importance to sexual reproductive success. For both *P. euphratica* and *P. pruinosa* populations, the number of days of flowering phenological period per population occupied more than half of the whole flowering phenological period and exhibited a long period of overlap. We found that a high level of asynchronism in flowering period among individual plants of the same sex caused by the differences in individual development within the population resulted in a great number of days of flowering period per population. Therefore, a relatively longer flowering period ensures continuous pollen dispersal from male plants and provides adequate time for female plants to complete pollination and fertilization. However, such flowering asynchronism implies a relatively sparse pollinating at a given time. Such lower but consistent pollination-related activities could effectively mitigate the impact of interruption of pollination and fertilization processes caused by adverse natural conditions, such as sudden decreases in temperature and a heavy rain. Consequently, this reproductive strategy appears to have been adopted by *P. euphratica* and *P. pruinosa* populations during their long-term adaptations to environmental changes.

The number of *P. pruinosa* flowers per male plant could reach 1056, and the number of pollen grains per flower could reach 2,770,988, confirming that the males provided sufficient pollen during reproductive stage (Liu et al., 2004). Li et al. (2002) found that the viabilities of pollen from *P. euphratica* and *P. pruinosa* could be maintained for 20 and 40 d, respectively, at a moderate temperature. We found that the peak flowering period of male plants was earlier than that of female plants. Therefore, we speculated that as long as pollen reached the stigma, pollen viabilities could be maintained throughout the flowering period of female flowers until fertilization. Therefore, despite an unbalanced numbers of female flowering plants and male flowering plants per day and asynchronism in their peak flowering periods, *P. euphratica* and *P. pruinosa* populations could still achieve a successful sexual reproduction by providing an adequate amount of pollen, maintaining pollen viability for an adequate duration, and ensuring a long overlap period between female and male flowering periods.

4.2 Relationship between flowering phenology and temperature

Many studies have suggested that phenology differences between species are due to different responses to temperature change, especially for the spring phenophase (Chmielewski and Rötzer, 2001; Fitter and Fitter, 2002; Zheng et al., 2006; Rosenzweig et al., 2008; Yang and Hou, 2008; Bai et al., 2009; Chang et al., 2009; Polgar et al., 2011; Huang et al., 2017). For a single species subjected to the same climatic condition, flowering phenology can be mainly attributed to genetics (Zhang and Chen, 2001), while variations in flowering phenology in different years might be due to inter-annual climate variations (Zimmerman and Gross, 1984; Xiao et al., 2004). Previous studies have demonstrated that the starting dates of phenology were significantly correlated with plant exposures to previous temperature conditions (Rosenzweig et al., 2008; Polgar et al., 2011). For example, a study by Bai et al. (2009) on the correlation between the phenology of woody plants in Guiyang in Southwest China and climate change suggested that the spring phenophase and average temperature in previous months were well correlated. Indeed, the most significant correlations of flowering phenology with average temperatures of previous months were observed. Moreover, in this study, at the beginning of March, the first flowering dates were significantly correlated with the average temperature in February. Huang et al. (2017) found that the annual average temperature significantly increased in Guiyang, and the first flowering dates of most plants exhibited an earlier trend. Our results revealed a strong correlation between different flowering phenological traits and average temperatures in previous ten days,

previous one month, and previous three months of flowering. As the average temperature increased, the number of days of flowering phenological period per population, number of days of flowering phenological period per plant and average number of days of flowering period per plant all decreased (Table 6). Under the same environmental conditions, the first and last flowering dates of *P. euphratica* and *P. pruinosa* populations during 2013–2015 were earlier than those of during 2001–2003 (Tables 1 and 2), confirming that the higher temperatures during 2013–2015 caused the advance of flowering period of two species.

5 Conclusions

The average temperatures in previous ten days, one month and previous three months before the spring phenophase affect the flowering periods of *P. euphratica* and *P. pruinosa* populations. Both species adapt to temperature changes by adjusting their first flowering dates, number of days of flowering phenological period per plant, and average number of days of flowering period per plant. The results reveal that the flowering phenological traits of *P. euphratica* and *P. pruinosa* populations are sensitive to temperature changes.

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